DIET-INDUCED COLOR CHANGE IN THE HAWAIIAN HAPPY-FACE SPIDER *THERIDION GRALLATOR*, (ARANEAE, THERIDIIDAE)

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ABSTRACT

The Hawaiian happy-face spider *Theridion grallator* Simon is a small spider, endemic to Hawaii, where it is found under leaves in the wet and mesic forests. The abdomen is pale, translucent yellow, but variable amounts of red, black or white pigment may be superimposed on this to generate a host of patterned morphs. The translucence of the abdomen may enhance crypsis against predators searching the underside of leaves; the variability in the superimposed pattern may serve to counteract the development of a search image by the predator. The present study documents plasticity in base coloration, which can change rapidly and markedly following ingestion of certain types of prey. This may be merely a consequence of abdominal translucence. But it is interesting to note that it adds a whole new dimension to the color polymorphism of the species.

INTRODUCTION

Color change in animals is a widespread phenomenon. It is generally associated with a change in physiological state. This in turn may be induced by ontogenetic or environmental changes, or stress. In spiders, color change is known to occur under a variety of circumstances. Ontogenetic modifictions are widespread, with the adult coloration being attained in the final molt (Bonnet 1933; Homann 1946; Millot 1949). More rapid changes in color pattern have been noted in spiders of the family Araneidae, which accumulate guanine beneath the cuticle during periods of starvation, thereby developing a pattern of opaque white blotches over the abdomen (Foelix 1979).

Reversible color change has been most extensively documented in the crab spider *Misumena vatia* (Clerck) (Packard 1905; Gadeau de Kerville 1907; Rabaud 1923; Gabritschevsky 1927; Weigel 1941; Hinton 1976). This spider is usually whitish and sits on white flowers. If it moves to a flower of another color it can, by transferring a liquid pigmented material to the cuticle, change to the color of its new substrate. However, the transformation takes about 10 days to occur, and it is limited to pastel yellows and pinks. Similar reversible color changes have been found to occur in other crab spiders (Heckel 1891; Bristowe 1958) as well as the lynx spider *Peucetia viridans* (Hentz) (Oxyopidae) (Neck 1978).

The most rapid reversible changes to date are found in various Araneid spiders, as a result of migration of chromatic inclusions or retraction of guanocytes

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(Blanke 1975). The Australian *Phonognatha wagneri* Simon, for example, drops from its web when disturbed, the abdomen simultaneously changing from cream to brown (Roberts 1936). A similar phenomenon has been documented in *Leucauge subgemma* Bos. et Str. and *Chrysso venusta* (Yaginuma) (Uyemura 1957), *Floronia bucculenta* (Clerck) (Bristowe 1958), *Gea heptagon* (Hentz) (Sabath 1969) and *Cyrtophora cicatrosa* (Stoliczka) (Blanke 1975).

Rapid color change following dietary ingestion has not been documented in spiders. In this paper I demonstrate the phenomenon in the Hawaiian happy-face spider *Theridion grallator* (Simon). *T. grallator* is a small (up to 4.5 mm) spider endemic to the Hawaiian Islands, where it inhabits the underside of leaves of a variety of plants, especially the native *Broussaisia arguta* (Saxifragaceae) and *Clermontia arborescens* (Campanulaceae). The spider has a base color of pale, translucent yellow, but may exhibit a variety of abdominal color patterns (red, black or white) superimposed on this base color. The predominant color morph has no pattern (or a series of small black dots only); patterned morphs, although generally less common, are diverse in form and extent of pigment.

The study was initiated following a chance observation: while monitoring marked spiders (paint marks on certain legs), I observed an individual change base coloration from translucent yellow to bright orange. Here I examine the nature of diet-induced changes in base color, and possible functions of the phenomenon. To what extent can spiders change the base color of the abdomen, and do prey items that are normally included in their diet induce reversible color change? The polymorphic nature of the pattern superimposed on the base color is considered elsewhere (Gillespie and Tabashnik in press).

METHODS

The rate and extent to which *T. grallator* is capable of changing its color was determined by keeping individuals in vials and allowing them to drink from cotton swabs saturated with food coloring (red, green, blue and black). Spiders in control vials had cotton swabs saturated with water only.

Individuals of *T. grallator* were then given a variety of insects that they might capture in their natural environment. These were primrily Diptera: Drosophilidae in the size range 2-4 mm ($N = 11$) and 5-6 mm ($N = 5$) and Dolichopodidae in the size range 2-4 mm ($N = 9$). Lepidoptera (one adult moth and two larvae), Homoptera (Cicadellidae, $N = 3$) and Araneae (Theridiidae, $N = 1$) were also used to determine their effect on the base color of *T. grallator*.

Field observations were made on populations of *T. grallator* in native forest (mixed Ohi'a—Koa) in the Nature Conservancy of Hawaii's Waikamoi Preserve on Maui, near the common boundary of the Preserve and the Makawao State Forest at 1360 m elevation. Spiders were located by thorough scrutiny of leaves of *Broussaisia arguta* and *Clermontia arborescens* in an area of approximately 1 hectare, and were marked with small dots of paint on a leg. Individuals were monitored once every two days between October 1987 and April 1988. Whenever a spider was found to be feeding on prey, it was watched for any subsequent color change. The duration of the color change (the period from the initial observation of feeding until it reverted to the original translucent yellow) was determined by checking color on sebsequent days. Color changes in marked

Table 1.—Change in color from pale yellow as a consequence of prey ingestion by the Hawaiian happy-face spider *Theridion grallator*. Spiders were fed prey collected from the Waikamoi study site. The color change induced in the opisthosoma of the spider by a particular prey item, and the duration of the color change before the spider reverted to pale yellow, were all recorded. N = number of spiders observed.

Prey	N	Color change	Duration (days)
DIPTERA			
Drosophila, 2-4 mm	11	Orange	2
Drosophila, 5-6 mm	5	Orange	3
Dolichopodidae, 2-4 mm	9	Orange	2
LEPIDOPTERA			
Adult moth	1	Dark orange	
Caterpillar	2	Green	4-6
HOMOPTERA			
Cicadellidae, 2-4 mm	3	Green	2-3
ARANEAE			
Theridiidae, 2-4 mm	1	Orange	2

spiders were also monitored when feeding was not directly observed. This allowed an estimate of the range of base colors the spiders could exhibit under natural conditions, and their relative frequency.

In order to determine the generality of the phenomenon of color change following dietary ingestion, species from two other genera of the Theridiidae and one from the closely related Nesticidae, were tested for color changes induced by intake of food coloring. The species were chosen on the basis of degree of pigmentation of the abdomen, and were all from southeastern Tennessee. *Nesticus barri* Gertsch is a pale, translucent yellow, esentially eyeless troglobite; it was collected from Lost Cove Cave, near Sewanee, Tennessee. *Achaearanea tepidariorum* (C. L. Koch), an extremely common spider found throughout the United States, has a dirty white abdomen with gray markings. *Latrodectus mactans* (Fabricius) has a shiny black abdomen, with a red "hourglass" mark on the venter. Both *A. tepidariorum* and *L. mactans* were collected in Sewanee, Tennessee. Individuals of each of these species (five *N. barri*, five *A. tepidariorum* and two *L. mactans*) were placed in vials with swabs of red and green food coloring (and water as control). Spiders were observed as they ingested the food coloring, and monitored for changes in color over the next 7 days. Individuals were then exposed to the second food color.

RESULTS

When placed in a vial, *T. grallator* readily ingested food coloring from the cotton swabs. The color could be seen running into the abdominal section of the intestine within 5-10 s, and infusing it with color within 1 min. The dye then accumulated in the Malpighian tubules before being excreted after an average of 3.5 (SD = 1.6) days.

A similar effect was found when *T. grallator* was fed prey collected from the Waikamoi study site. Table 1 summarizes the color changes that were observed. The color generally changed from translucent yellow to either orange (following ingestion of various Diptera or adult Lepidoptera) or green (after ingestion of larval Lepidoptera and adult Homoptera). The abdomen retained the color for 2-

Table 2.—Overall frequency of color changes in natural populations of *T. grallator*: marked individuals that were found to have changed color, whether or not the prey capture event itself was observed ($N = 82$). Where prey capture was observed ($N = 11$), the approximate duration of each color change (to the nearest day) was determined. The prey inducing the change of color to chocolate was observed on neither occasion; but both these spiders retained their color for 7 days after the change was initially observed.

Color	Proportion	Average duration (days)
Orange	81%	2-4
Green	17%	4-6
Chocolate	2%	>7

6 days, retention time probably being a function of the amount of pigment ingested.

The frequency of color changes in natural populations of *T. grallator* (marked individuals that were found to have changed color, whether or not the prey capture event itself was observed) are shown in Table 2. As can be seen, the most common color change was that from translucent yellow to orange, reflecting the fact that small dipterans comprise approximately 70% of the dietary intake of *T. grallator* (Gon 1985). On two occasions, the base color was found to have changed to very dark chocolate brown. It is not known what prey item these individuals had consumed.

The three other species tested for susceptibility to color change following ingestion of food coloring varied widely in their response. *N. barri* changed color in a manner similar to *T. grallator*. The red and green food coloring suffused the abdomen within 1 minute; the dye was excreted after 2-3 days (average 2.7 days). *A. tepidariorum* showed a definite, but very much weaker, response. The colors became interspersed between the white dots of guanine, giving a mottled appearance to the abdomen. In *L. mactans*, the food coloring could be seen as a slight red or green tinge to the black abdomen. The color did not suffuse the abdomen, but rather appeared as a folium, the pattern probably dictated by the digestive diverticula.

DISCUSSION

The Hawaiian happy-face spider is capable of passively changing base coloration according to dietary intake. Such rapid and reversible color changes following ingestion have never before been documented in spiders. But, as I have shown here, other species of spiders can also change color when they ingest dyes. The degree to which spiders are capable of diet-induced color change appears to be a function of their translucence. The heavily pigmented *L. mactans* showed a barely discernible color change. In *A. tepidariorum*, the ingested dye was seen as spots interspersed between the natural pigment and guanine crystals on the abdomen. Under natural conditions, pigments from prey will tend to be ingested in much smaller amounts, and their effects on abdominal coloration considerably more subtle. In *N. barri*, however, the ingested dye suffused the entire abdomen in a manner similar to that observed for *T. grallator*. *N. barri* may also demonstrate observable color change under natural conditions if it ingests pigmented prey. Indeed, although prey capture was not observed, two individuals

of this species have been found in the cave with black (as opposed to the usual pale, translucent yellow) abdomens.

What are the selective forces responsible for degree of pigmentation in spiders? Nearly all spiders—in common with insects—have some kind of integumental pigment, which may serve to protect them from radiation (ultraviolet), to regulate temperature, and may also function in protection from predation (Holl 1987). Complete depigmentation is a characteristic of obligate cavernicoles (Gertsch 1984). Yet *T. grallator*, an inhabitant of the Hawaiian forests, has a translucent base color similar to the troglobitic *N. barri*. What evolutionary forces might be implicated in the loss of pigment in this terrestrial species?

One of the most abundant groups of insectivores in Hawaiian forests are the honeycreepers (Perkins 1913). In Maui's Waikamoi Preserve, the most common insect gleaner is the Maui Creeper, *Parareomyza montana*, whose behavior of searching the underside of leaves resembles that of the creeper family Certhidae (Scott et al. 1986). *T. grallator* occupies the underside of leaves. To the human eye, the translucence of these spiders renders them almost invisible against the light filtering through the leaf when viewed from below. Birds may encounter the same difficulty when searching for prey. Avoidance of predation may well have played a major role in the depigmentation of *T. grallator*.

Diet-induced color change in *T. grallator* may merely be an inevitable consequence of its translucence. Yet it is interesting to note that this spider is highly polymorphic. Although the base color of the abdomen is translucent yellow and many individuals exhibit this base color alone, others exhibit a host of superimposed patterns of red, black and white patches. These patterns are under genetic control and are inherited as a simple Mendelian trait (Gillespie and Tabashnik in press). Diet-induced color change adds an entirely new dimension to the enormous array of color morphs that the species can exhibit. Could there be any advantage to an individual in widening its spectrum of color morphs?

If there is any selective force operational here, it is most likely to be the avoidance of predtion by birds. A common tendency in birds is the development of a search image (Clarke 1962; Allen 1974, 1976; Murdoch and Oaten 1975; Atkinson and Warwick 1983; Greenwood 1984; but see Guilford and Dawkins 1987). Studies have implicated the development of such search images in the generation of interindividual variability in color patterns of the prey involved (Endler 1978; Rettenmeyer 1970). Selection under these conditions will tend to favor the less common morphs, which will consequently increase until numbers are sufficient to allow the avian predators to develop a search image towards them. It is possible that strong selection for abnormal color patterns is the primary selective force generating variability in coloration of *T. grallator*, whether this is genetically determined or environmentally plastic—a passive consequence of dietary ingestion.

ACKNOWLEDGMENTS

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